

A multifaceted approach to modelling growth of the Australian bonito, *Sarda australis* (Family Scombridae), with some observations on its reproductive biology

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Abstract. Growth of the Australian bonito, *Sarda australis*, is described for the first time using data from three different sources. Von Bertalanffy growth functions were fitted to: (1) size-at-age data derived from sectioned sagittal otoliths, (2) monthly length–frequency collections from a commercial line fishery, and (3) tag–recapture data from a long-term cooperative tagging study. Age estimates of *S. australis* were indirectly validated by examining the percentage of otoliths with opaque edges each month. The best-fitting growth functions for each data source yielded similar results, showing strong seasonal variations in growth rate. Maximum growth occurred during summer, with near cessation of growth apparent during winter. Early growth was very fast, with fish attaining ~30 cm fork length (FL) after 3–4 months. Growth of males and females was not significantly different. The oldest fish sampled was estimated to be 3+ years old, while the largest fish aged was 63.8 cm FL. Gonadosomatic indices indicated that *S. australis* has an austral spring/summer spawning period in eastern Australia. A preliminary estimate of the size at first sexual maturity was ~36 cm FL for both males and females, corresponding to an age of ~1 year.

Additional keywords: age, cohort, fishery, otolith, tagging.

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Introduction

Bonitos, genus *Sarda*, are intermediate-sized members of the teleost family Scombridae distributed globally throughout tropical and temperate seas (Yoshida 1980). The genus is characterised by epipelagic, schooling species that are important to both commercial and recreational fisheries (Collette and Nauen 1983). There are four species within the genus *Sarda* – the Atlantic bonito, *Sarda sarda* (Bloch, 1793); the striped bonito, *Sarda orientalis* (Temminck & Schlegel, 1844); the Australian bonito, *Sarda australis* (Macleay, 1881); and the Pacific bonito, *Sarda chiliensis* (Cuvier, 1832) – with northern and southern Pacific bonito subspecies recognised: *S. chiliensis lineolata* (Girard, 1858) and *S. chiliensis chiliensis* (Cuvier, 1832), respectively. The Atlantic and Pacific bonitos support large fisheries and have been more extensively studied than other species within the genus.

A recent review of *Sarda* concluded that growth estimations within this genus were problematic because of the different methods used and the variable results obtained (Orsi Relini *et al.* 2005). Direct methodologies employed to estimate size-at-age have included counting annuli in whole otoliths (Campbell and Collins 1975; Rey *et al.* 1986; Ates *et al.* 2008), dorsal spines

(Rey *et al.* 1986; Zaboukas and Megalofonou 2007; Valeiras *et al.* 2008) and vertebrae (Rey *et al.* 1986). Curiously, no published studies have used sectioned otoliths to estimate size-at-age within *Sarda* despite the general agreement that sectioned otoliths produce more accurate and precise estimates (Campana 2001). Indirect methods to model growth have included analysis of length–frequency distributions and tag–recapture studies (Campbell and Collins 1975). Despite the variable results in terms of growth rate trajectories and longevity within *Sarda* (Orsi Relini *et al.* 2005), growth is generally reported to be rapid, with longevity less than 5 years (Orsi Relini *et al.* 2005; Ates *et al.* 2008).

Sarda australis occurs in the western Pacific Ocean where it is restricted to waters around south-eastern Australia, Norfolk Island and northern New Zealand (Collette and Nauen 1983). It is an important target of recreational fishers and there is an established commercial line fishery along south-eastern Australia. Landings in the commercial line fishery fluctuate annually between ~100 and 250 tonnes (Rowling *et al.* 2010) while the annual recreational harvest is in the order of 40–110 tonnes (Henry and Lyle 2003). In a review of the biology and fisheries of *Sarda* species, Yoshida (1980) highlighted the

paucity of information on the growth of *S. australis* and recommended it as a research priority. Unfortunately, there has been no biological research on *S. australis* since that time. Given the importance of the genus to fisheries worldwide, and the importance of *S. australis* in Australia, the aim of this study was to describe the growth and longevity of *S. australis* in eastern Australian waters. We tested the hypotheses that growth (in terms of length) of *S. australis* varies with sex and also with season. We also tested the hypothesis that modelling from three different data sources would yield comparable descriptions of growth. In addition, further information important for the management of the species, including preliminary estimates of seasonality of spawning and size at maturity, are reported.

Materials and methods

Growth of *S. australis* was described using 3 different methodologies: (1) size-at-age estimates derived from enumerating annuli in sectioned otoliths, (2) analysis of monthly length–frequency distributions, and (3) changes in fish length through time from a tag–recapture program. Commercial catches were used to obtain samples for the first two methods as well as for information on the reproductive biology of *S. australis*.

Biological sampling

Sarda australis was sampled from commercial landings between February 2004 and September 2009. For each specimen the length (fork length – FL) to the nearest millimetre, sex (through macroscopic appearance of the gonads) and gonadosomatic index (GSI – gonad weight as a percentage of total bodyweight) were recorded and the sagittal otoliths were removed. The time of year when *S. australis* reproduce was estimated by plotting the mean monthly GSI values each month for each sex. The size at first sexual maturity was estimated using two methods: (1) by plotting GSI versus FL to determine the size at which GSI levels rise, and (2) using the empirical equation of Froese and Binohlan (2003), which relates size at maturity to asymptotic length:

$$\log_{10} L_m = 0.8979 \times \log_{10} L_\infty - 0.0782$$

where L_m is the mean length at first maturity and L_∞ is the mean asymptotic length.

Age-based growth

The sagittal otolith pairs from 251 *S. australis* were weighed and one of each pair was embedded in resin and a series of transverse cross-sections (~350 µm in thickness) were cut using a Gemmasta™ lapidary saw fitted with a diamond-impregnated blade. This method ensured that at least one cross-section was made through the otolith core (primordium). Sections were polished on both sides using a manual polishing machine (LaboPol-4, Struers) with 1200 grit paper (SiC paper, Struers) and mounted using resin on a glass microscope slide under a coverslip. Ages were estimated by counting opaque zones that were observed on either side of the sulcus when viewed under reflected light against a black background (Fig. 1). Counts of opaque zones were made independently by two readers and a consensus count decided upon involving a third reader.

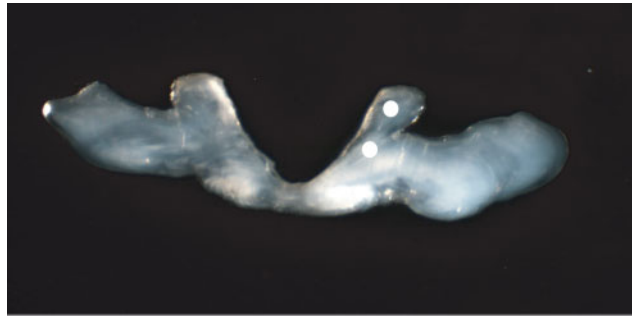


Fig. 1. Transverse section of an otolith of *Sarda australis* viewed under reflected light. The fish was a female of 53.9 cm fork length that was captured during January. Two opaque zones were counted and the edge determined to be translucent.

All otoliths were reread by the lead author to allow an estimate of precision. A decimal age was calculated as the number of completed opaque zones (assumed to be annual) plus the proportion of the year after the designated birthdate for *S. australis* in eastern Australia (November, see Results). The edge of each otolith was characterised as being either opaque or translucent and plots of the percentage of otoliths with opaque edges each month were used to indirectly validate that opaque zones formed annually.

Growth was modelled by fitting two versions of the von Bertalanffy growth function (VBGF) to the size-at-age data. The first VBGF was the specialised version (von Bertalanffy 1938):

$$L_t = L_\infty (1 - e^{-k(t-t_0)})$$

where L_t is the length at age t , L_∞ is the mean asymptotic length, k is the rate at which the curve approaches L_∞ , and t_0 is the theoretical age of the fish at zero length.

The second VBGF included parameters that described seasonal variation in growth rate (Gayanilo and Pauly 1997):

$$L_t = L_\infty \{1 - e^{-k(t-t_0) - (ck/2\pi)[\sin 2\pi(t-t_s) - \sin 2\pi(t_0-t_s)]}\}$$

where c is the amplitude of oscillation ranging between 0 and 1 and t_s is the summer point or when growth rate is maximised ranging between 0 and 1.

Growth curves were compared, across equal size and age ranges, using the Akaike information criteria (AIC) (Akaike 1973; Imai *et al.* 2002). An AIC value was calculated for each curve based on the number of parameters and goodness of fit. To compare growth curves between sexes an AIC value was calculated for the separate curves, and then for a model based on the combined data and a single curve. The AIC values were then used to derive an AIC weight (wAIC), the plausibility of that being the best fit based on the models presented. The wAIC ranges from 0 to 1, with a value of 1 indicating complete support for that model (Akaike 1973).

Length–frequency analysis

The lengths (FL to the nearest whole centimetre below the true length) of *S. australis* landed by the commercial fishery were measured at the Sydney Fish Markets and regional cooperatives

between January 2005 and December 2008. The data were pooled by month across all years for analysis. Cohorts were initially identified through modal progression analysis of length distributions using the method of [Bhattacharya \(1967\)](#) and the software FiSAT II ver. 1.2.2 ([Gayanilo et al. 2005](#)). The routine NORMSEP (normal distribution separator) within the FiSAT application was then applied to refine estimates of the means and standard deviations of each cohort. The NORMSEP method separates cohorts using a maximum-likelihood method ([Hasselblad 1966](#)). As *S. australis* could not be sexed due to commercial handling practises, sex-based comparisons of growth were not possible with this method.

Similar to the age-based assessment of growth, the age of each cohort was assigned using the proportion of the year after the designated birthdate (November, see Results) that the monthly sample was taken. The resulting mean size-at-age data for each cohort was used to describe growth using the seasonal VBGF described above.

Tag-recapture study

Between 1974 and 2008, 13 075 *S. australis* were tagged and released as a part of the New South Wales (NSW) Fisheries Gamefish Tagging Program. This program involves volunteer recreational anglers (usually associated with angling clubs) to tag and release fish (see [Gillanders et al. 2001](#) for a full description of methods). The type of length measurements of fish at release and recapture was not recorded; however, it was assumed to be total length (TL) as this is the usual practice amongst recreational anglers in Australia. To allow comparison with the other VBGFs, TLs were converted to FLs using the relationship:

$$FL = 0.8453 * TL + 2.1212$$

($r^2 = 0.99$), derived during the present study.

The data on changes in length and time at liberty were used to model growth using the procedure outlined in [Francis \(1988\)](#). The earliest recapture used to model growth was tagged on 4 December 1980, and so, for convenience, 1 December 1980 was allocated as Day 1 in the analysis. Francis' procedure uses growth increment data from tag-recapture studies to describe mean annual growth ($g1$ and $g2$) at two lengths ($y1$ and $y2$), that are chosen to span the range of lengths in the data. The von Bertalanffy growth function parameters were then calculated from these parameters ([Francis 1988](#)). The growth model can incorporate parameters that describe growth rate variability (v), seasonal variation in growth (u and w , both set to range between 0 and 1), measurement error (m and s) and outliers (p) in the data. The parameters that describe measurement error (m) and measurement error standard deviation (s) were estimated from the tag-recapture data using records from fish that were recaptured within 30 days of being tagged (see [Gillanders et al. 2001](#)), the assumption being that the length at recapture should be similar to the length at release, as measurable growth is likely to be negligible within 30 days. Initially, a four-parameter model ($g1$, $g2$, m and s) was fitted to the data by minimising a log-likelihood function ([Welsford and Lyle 2005](#)). Plots of residuals against expected growth increment were examined to assess the fit of the model. Additional parameters were then added in a

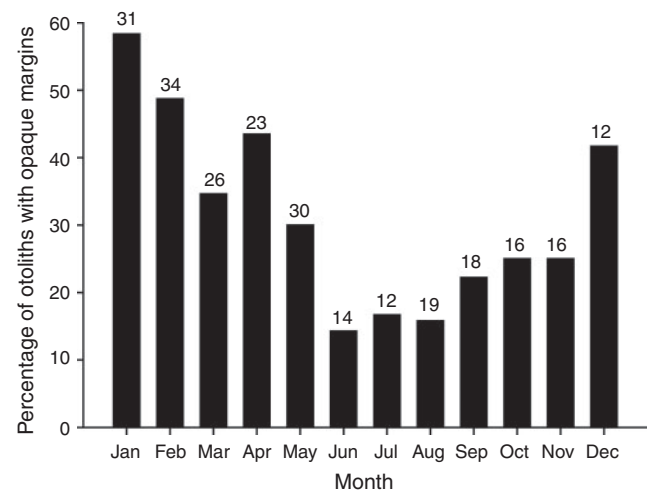


Fig. 2. The percentage of otoliths of *Sarda australis* with opaque otolith margins each month. The numbers are sample sizes each month.

stepwise procedure by selecting the parameter that gave the greatest increase in negative log-likelihood. The addition of one or two parameters was required to increase the negative log-likelihood by at least 1.92 or 3.00 respectively, to significantly improve the model fit ([Francis 1988](#)). Confidence intervals were estimated for each parameter by bootstrapping the dataset 1000 times and, to account for any skew in the distribution of bootstrap parameter estimates, a first-order correction for bias was performed as described in [Haddon \(2001\)](#) and [Welsford and Lyle \(2005\)](#). This correction was carried out on the basis of the proportion of bootstrap estimates that were less than the 'best estimate'.

Results

Age-based growth

In total, 251 *S. australis* were aged during the study. The mean coefficient of variation rereading the otoliths was 9.0%. The oldest *S. australis* sampled was estimated to be 3.5 years old and was 47.4 cm FL. The longest fish sampled was 63.8 cm FL and was estimated to be 3.4 years old. The percentage of otoliths with opaque edges each month showed a pattern consistent with annual periodicity of opaque zone formation ([Fig. 2](#)). The greatest percentages of otoliths with opaque edges were observed during the summer months before declining during autumn and being lowest during winter.

There were no differences in growth rates between males and females, determined by the lack of improvement to the model fits when examining the sexes separately. This was the case for both the specialised (wAIC = 0.96 for the pooled specialised curve) and seasonal (wAIC = 1.0 for the pooled seasonal curve) VBGFs. The data for sexes were therefore combined and a comparison of the specialised and seasonal versions of the VBGF indicated that the seasonal version was a better fit (wAIC = 1.0 for the seasonal model) ([Fig. 3](#)). The amplitude of seasonal growth (C) was equal to 1, which is the upper constraint put on this parameter as it is the maximum before the model predicts negative growth. The period of maximum growth (t_s) was equal to 0.09, which if calculated from a peak

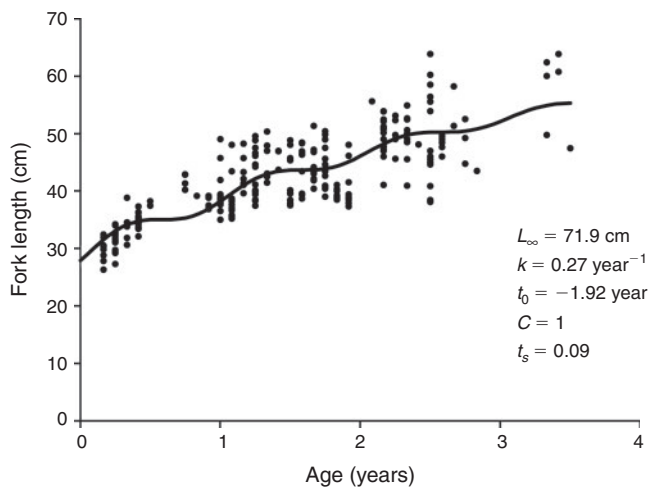


Fig. 3. Size-at-age data for *Sarda australis* with fitted seasonal von Bertalanffy growth function.

spawning period of November (see below), equates to a December peak in growth rate.

Length–frequency analysis

The monthly length–frequency distributions showed multiple modes, which were assumed to represent yearly cohorts (Fig. 4). Small modes of fish (mean <30 cm FL) were evident during February, April and July; however, these small modes were hypothesised to represent fish from multiple spawning events within the main spawning season, were not fully recruited to the fishery and were therefore not used to model growth. Assuming a general birth month of November for *S. australis* off central NSW (see below), the 0+ cohort was evident with a mean size of 30.9 cm FL in January (Fig. 4). This cohort increased in mean size through the year to 38.1 cm FL by October when 12 months old.

Similar to the otolith-based growth curves, a seasonal VBGF provided the best fit to the data (wAIC = 1.0 for the seasonal curve), with the parameter describing the amplitude of seasonal growth (C) equal to 1, and the period of maximum growth (t_s) equal to 0.24, which, if calculated from a peak spawning month of November, equates to a February peak in growth rate. The remaining VBGF parameters were estimated to be: $L_\infty = 129.2$ cm FL; $k = 0.11$ year⁻¹; and $t_0 = -2.26$ years.

Tag/recapture study

In total, 150 *S. australis* were recaptured between 1980 and 2008 and, of these, 110 had information on their lengths at release and recapture and the time between tagging and recapture. Time at liberty ranged from 2 to 765 days and sizes at tagging ranged between 25 and 66 cm. Recaptures were recorded from between the Gold Coast in Queensland (27.56°S) and Gabo Island in Victoria (37.34°S), covering most of the latitudinal range of the species. The furthest distance between release and recapture was ~850 km: a fish that was tagged in September 1991 at Southport, Queensland (27.56°S) and was recaptured in April 1992 at Ulladulla, NSW (35.20°S).

The greatest growth recorded was 21 cm, for two fish, both of which were reported to be 40 cm when tagged and at liberty for

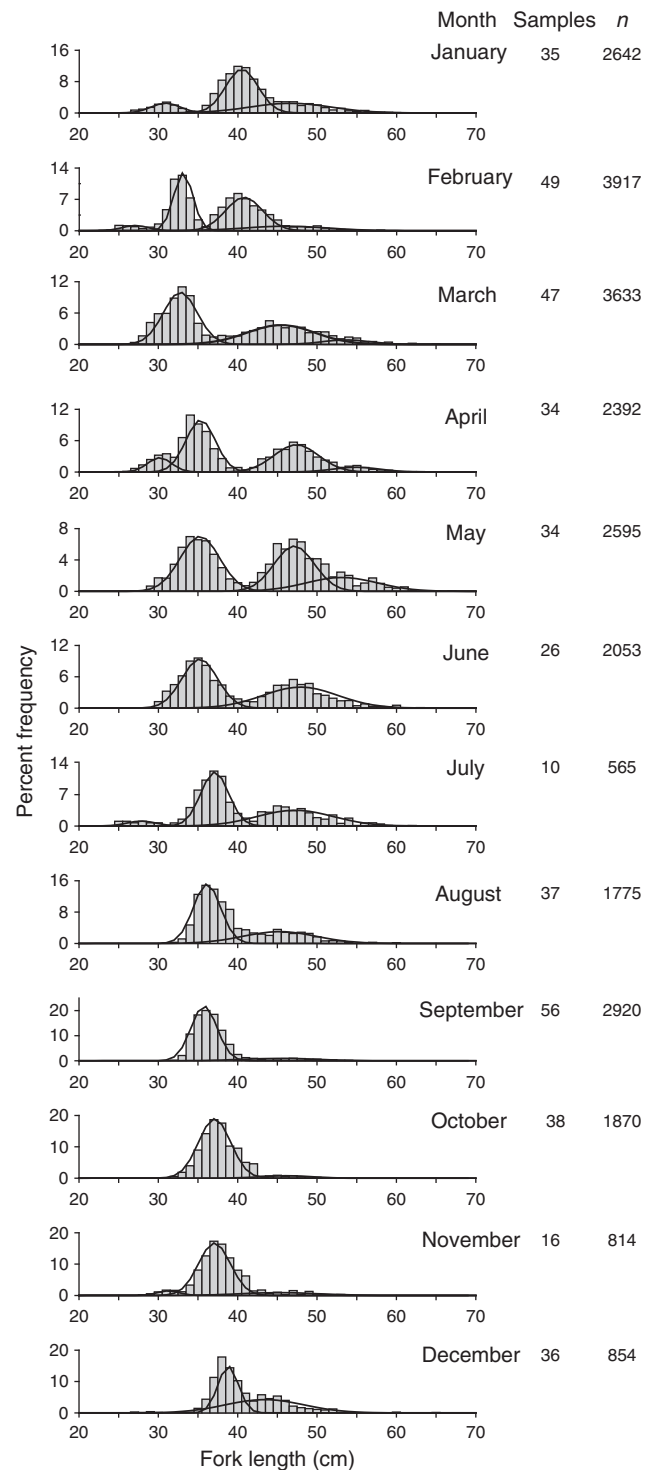


Fig. 4. Length–frequency distributions of *Sarda australis* measured from commercial landings (histograms). n is sample size. The normal distributions fitted to modes are indicated by solid lines.

484 and 765 days, respectively. The sizes of fish tagged and recaptured showed large peaks at 5-cm intervals (Fig. 5), suggesting that many fish had their lengths estimated by fishers. Mean sizes (cm TL with standard deviations) at tagging and

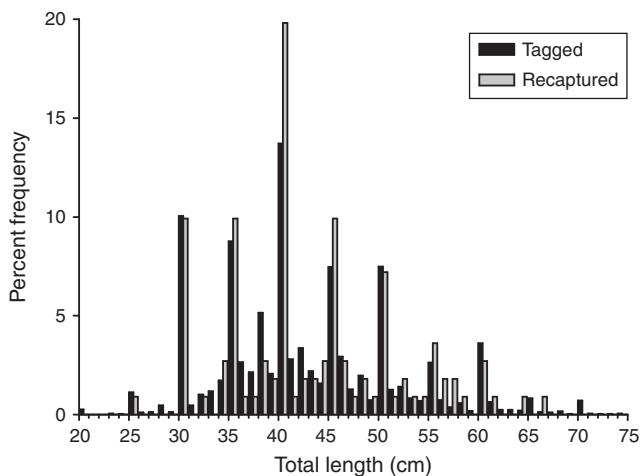


Fig. 5. The length distributions of *Sarda australis* tagged and recaptured.

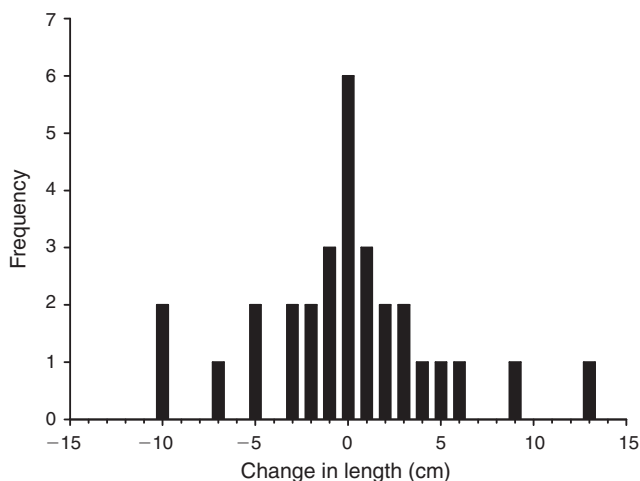


Fig. 6. Change in length of tagged *Sarda australis* that were recaptured within 30 days of release.

recapture were 42.67 cm (9.95) and 43.23 cm (9.23), respectively. The shape of the distributions were not significantly different (Kolmogorov–Smirnov test, $P > 0.05$), suggesting that tagging did not affect the chance of recapture at any size.

The parameters describing measurement error (mean m and standard deviation s) were estimated using those recaptures that occurred in fewer than 30 days from release ($n = 30$). Two records were removed from the dataset because of unrealistically large increases in length (15 and 19 cm) in fewer than 30 days. The resulting data were approximately normally distributed around 0, with a mean of 0.00 and a standard deviation of 4.86 (Fig. 6), suggesting that considerable measurement errors existed but without bias.

The best-fitting model described growth in terms of mean annual increases in length at 30 and 60 cm (g_{30} and g_{60}), measurement error (m and s) and seasonal growth variation (u and w) (Table 1). The addition of parameters describing growth rate variability (v), and outliers (p) did not result in significant improvements to the model. The best-fitting model

Table 1. Parameter estimates describing growth for *Sarda australis* from tag–recapture data

Parameter	Estimate	95% CI
L_{∞} (cm FL)	61.94	57.67–79.44
k (year ⁻¹)	0.64	0.28–1.26
$y1$ (cm)	30	
$y2$ (cm)	60	
g_{30} (cm)	15.03	9.28–20.74
g_{60} (cm)	3.65	2.20–5.02
u	0.97	0.16–1.00
w	0.24	0.11–0.41
s	4.86	
m	0	
–veLLike	334.71	

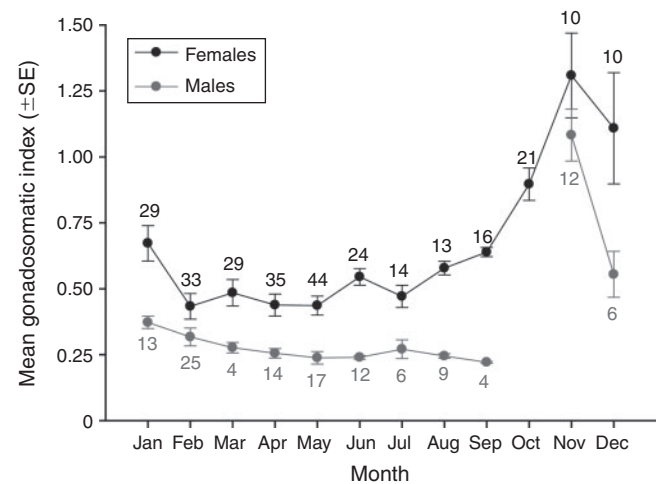


Fig. 7. Mean (\pm s.e.) monthly gonadosomatic indices for female and male *Sarda australis*. The numbers are sample sizes each month.

indicated annual growth rates of 15.0 and 3.7 cm for 30 and 60 cm fish respectively. The parameter w , which describes the time of year that growth is maximised, was 0.24. This fraction of the year after Day 1 of the tagging study (1 December 1980) equates to a February peak in growth. The parameter u , which describes the amplitude of seasonal growth, was 0.97. This value indicates near cessation of growth six months after the period of peak growth. Plots of residuals against expected growth increment showed no patterns (correlation 0.01), suggesting that the growth model was appropriate (unpubl. data).

Biological assessment

The length to weight relationship for *S. australis* was described by the power relationship:

$$\text{Bodyweight (g)} = 0.0125 \times \text{FL(cm)}^{3.0584},$$

($r^2 = 0.97$).

The gonads of *S. australis* were at their largest relative to body weight during the austral spring/summer months, with mean GSIs peaking during November (Fig. 7). The highest

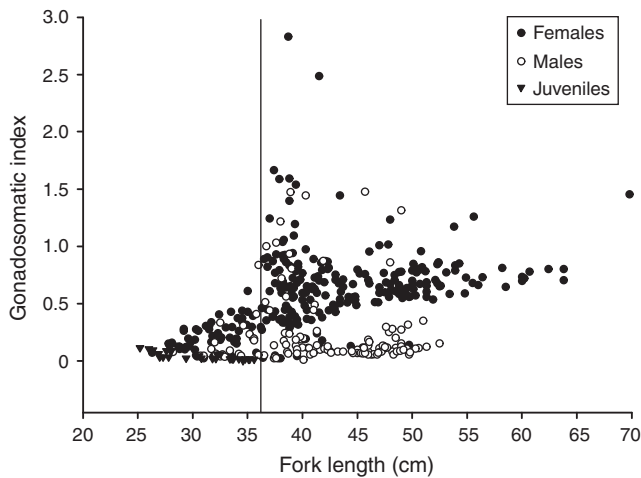


Fig. 8. Gonadosomatic indices versus fork length for female and male *Sarda australis*.

individual GSI values observed for females were 2.5% and 2.8%, sampled during November and December 2008, respectively. During November, the mean male GSI value (1.0%) was similar to that for females (1.3%); however, mean GSIs for males were considerably lower than those for females during all other months (Fig. 7).

The plot of FL versus GSI indicated elevated GSI values (arbitrarily $>0.5\%$) for both sexes after ~ 36 cm FL (Fig. 8). Without knowledge of what level of GSI is associated with spawning in *S. australis*, this observation supports the model that sexual maturity occurs at approximately this size in both sexes. This estimate compares favourably with the empirical relationship of Froese and Binohlan (2003), which indicated the size at sexual maturity of between ~ 34 and 38 cm FL from the tag-recapture and age-based estimates of L_{∞} respectively.

Discussion

Sarda australis appears similar to all other species of *Sarda* in exhibiting rapid growth and with longevity generally <5 years. The estimates of growth rates based on size-at-age data and length-frequency modal progression analysis indicated extremely fast, yet variable, growth during the first few months after hatching. The size-at-age-based model indicated ~ 33 cm FL after three months and the length-based model indicated a length of ~ 32 cm FL after this time. Similarly, Rey et al. (1986) reported *S. sarda* to grow at between 3 mm and 4 mm day^{-1} during its first three months of life, which would produce lengths of 27 – 36 cm after three months in that species. Sporadic sampling of juvenile *S. orientalis* between 161 and 348 mm in the wild have similarly indicated a mean growth rate of 2.6 mm day^{-1} (Yoshida 1980). In aquaculture conditions, larval *S. orientalis* grew to 14 mm in length after 10 days, 106 mm in 30 days, 219 mm in 42 days and 290 mm after 99 days, which equated to a mean daily growth rate of ~ 2.9 mm day^{-1} (Yoshida 1980).

Each method used to describe growth in *S. australis* indicated substantial variation in growth rate throughout the year (Fig. 9). All methods indicated that growth rates were fastest during the

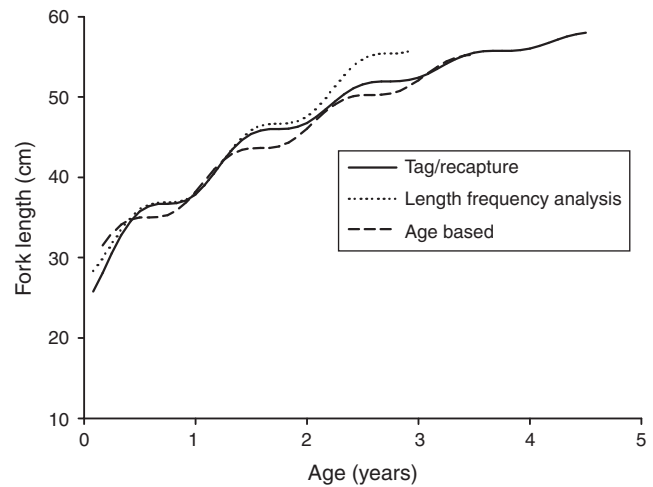


Fig. 9. Seasonal von Bertalanffy growth functions for *Sarda australis* derived from three different data sources. Growth functions are plotted from the minimum age to the maximum size of fish in each dataset.

summer months and declined to almost zero during the winter months. Such large seasonal variation in growth is often reported (Pauly et al. 1992) and appears to be a feature common to species of *Sarda*. *S. chiliensis* (Campbell and Collins 1975) and *S. sarda* (Ates et al. 2008) have also been shown to exhibit almost zero growth during the winter months. The cause of the near cessation of growth, at least in length, of *Sarda* spp. during the winter months is unknown, but is likely related to factors such as water temperature, food availability and reproductive condition. It is also feasible that all available energy resources are partitioned into gonadal development during the winter months leading up to a spring spawning.

Each of the methods used to model growth in the current study has advantages and disadvantages that need to be considered. Using size-at-age data from sectioned otoliths is the only method of the three used that easily enables comparison of growth between sexes, as the other methods do not directly allow the determination of sex during data collection without additional time consuming and expensive fish dissections. However, *Sarda* spp. have very small, fragile otoliths that are difficult to extract, handle and interpret (Furlani et al. 2007). The degree of precision observed during the present study (mean CV of 9%) is low amongst fish ageing studies (Campana 2001) and reflects the difficulty in ageing species from this genus. The length-based assessment of growth can be relatively cheap to sample; however, the method is reliant on the correct identification of cohorts through time. The large individual and seasonal variation in growth rates of species like *S. australis* may make this difficult. However, our approach of combining length-frequency distributions across years may, in fact, improve average growth estimates, particularly for younger cohorts, of *S. australis*. This is because potentially large interannual variations in growth will be smoothed, therefore producing cohorts with more accurate average sizes for any given age. The identification of older cohorts, however, with relatively few fish in the length distributions and a higher degree of overlap in the sizes of multiple cohorts with age, may be difficult. Importantly, the selectivity of the hook and line fishery is unlikely to

be biased towards catching any particular size-class of *S. australis* (Lokkeborg and Bjordal 1992), therefore making length-based monitoring of fishery landings largely representative of the stock being fished. Third, the tag–recapture data can describe growth of individuals only between the time of tagging and subsequent recapture. The recreational tagging study used here had a very low recapture rate of individuals with useful information on growth (110 fish from 13 075 tagged, or 0.8%). In addition, the data were collected through almost three decades (1974 to 2008) and considerable measurement error was apparent. Despite this, there was no evidence of bias within the data collected, which is an important consideration when assessing the usefulness of such cooperative recreational tagging programs. Indeed, Gillanders *et al.* (2001) concluded that such tagging programs were suitable for obtaining useful biological information, but that they should have clearly identified scientific objectives and quality control. A useable recapture rate of <1% of tagged individuals raises questions regarding the cost-effectiveness of continuing to tag *S. australis* as a part of this program. The factors contributing to the very low recapture rate for this species are unknown and should be the focus of future study. Factors to be examined could include tag loss, non-reporting of recaptured fish, and post-release mortality.

Given the high degree of concordance in growth estimates between methods over the sizes and ages considered, and the similarities in growth rates compared with other members of this genus, it is concluded that each of the methods used produced plausible growth estimates for *S. australis*. It is important to note, however, that while growth may be well described over the sizes and ages considered, that the VBGF parameters may not describe growth well over all ages. For example, the length–frequency derived estimate of L_{∞} of 129.2 cm FL is clearly too large given the maximum reported length of 101 cm FL (Collette and Nauen 1983). In addition, the estimates of the parameter t_0 of ~ -2 years suggest that early growth is not being well described. These issues highlight the importance of acknowledging the size and ages over which growth is being modelled and some of the limitations of the VBGF for describing growth rates in species with growth characteristics similar to those of the genus *Sarda*.

The general agreement in growth rates between methods also supports our validation of the age-based otolith data. However, the largest fish sampled in our age-based study was only 63.8 cm FL and the oldest was estimated to be 3.5 years old, whereas other species of the genus have been reported to attain longevities of up to 6 or 7 years (*S. chiliensis*: Campbell and Collins 1975; *S. sarda*: Zaboukas and Megalofonou 2007). It is therefore possible that each of our data sources did not capture growth of the largest individuals. However, considering that our samples were sourced from more than 14 000 fish during nearly three decades and from both commercial and recreational sectors, it is more likely that animals larger than those sampled are very rare in the population sampled off the NSW coast.

Sarda australis has an austral spring/summer spawning period peaking in November. Similarly, *S. chiliensis* from Chile also has a spring/summer spawning period (Goldberg and Mussiott 1984). Interestingly, the maximum GSI values observed for *S. australis* were considerably lower than those

reported for *S. sarda* and *S. chiliensis* during their respective spawning seasons. The highest mean GSI value for female *S. australis* was 1.3% during November; however, Orsi Relini *et al.* (2005) reported mean GSIs of >5% with individual GSIs of up to 12% for *S. sarda*. Similarly, Black (1979) and Goldberg and Mussiott (1984) reported mean GSIs of between ~ 5 and 9% for *S. chiliensis*, with individual GSIs of up to 10%. The reason for the comparatively low GSIs observed for *S. australis* in the present study may be due to differences in reproductive biology within the genus. Alternatively, this variation could be a result of not sampling *S. australis* when spawning was actually occurring. However, samples of *S. australis* were collected over a large part of their geographic distribution and through all months of the year, albeit mostly from the inshore commercial line fishery. Some other small scombrids such as the little tunny, *Euthynnus alletteratus* (Rafinesque, 1810), also have maximum GSIs of <2% reported (Kahraman *et al.* 2008). It is clear that more work is required in order to improve our understanding of the reproductive biology of *S. australis*.

The size at sexual maturity for *S. australis* was estimated to be ~ 36 cm FL based on the size at which markedly elevated GSI values occurred. These elevated GSI values were apparent at this size for both males and females, suggesting no difference in the size at sexual maturity between sexes. This estimate was similar to those calculated using the empirical relationship between size at maturity and L_{∞} estimates from the tag–recapture and age-based growth models of ~ 34 – 38 cm FL. Despite the preliminary nature of the investigations into reproductive biology, these estimates of size at maturity are consistent with those reported in other species of *Sarda*. The estimated size at maturity for *S. australis* corresponds with the mean size of the 1+ year cohort during November and suggests that this species matures at 1 year of age. Sexual maturity has also been reported to occur within the first year of life for *S. sarda* (Ates *et al.* 2008) and in nearly 100% of *S. chiliensis* by age 2 years (Black 1979).

Several findings in the present study highlight deficiencies in our understanding of the distribution and seasonal movements of *S. australis*. All sampling was done off the coast of NSW, an area that encompasses most of the species' distribution and represents most of the fishery. The tag–recapture data demonstrated that *S. australis* is highly mobile, which is likely to maintain a well mixed population, as is hypothesised for *S. sarda* (Orsi Relini *et al.* 2005). However, a consistent lack of larger modes of fish landed by the commercial fishery during September–November each year, the inability to sample fish approaching the maximum reported size, and the relatively low maximum GSI levels recorded when compared with other species of *Sarda*, leads to the hypothesis that the largest *S. australis* move away from the inshore coastal areas off NSW during spring/summer and that these fish spawn during that time. It is clear that more work is needed to understand the population dynamics and movement patterns of *S. australis* before the growth estimates presented here can be further refined.

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